

PUPAE OF THE CRANE FLY GENUS *LEPTOTARSUS*  
(DIPTERA: TIPULIDAE) IN THE NEW WORLD, WITH  
DISCUSSION OF THE MONOPHYLY OF THE GENUSJON K. GELHAUS<sup>1</sup>

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## ABSTRACT

The pupae of the *Leptotarsus* subgenera *Limoniodes* and *Pehlkea* are described, diagnosed, and illustrated for the first time from specimens collected in Ecuador. The pupa of *Leptotarsus* (*Longurio*) *testaceus* from eastern North America is redescribed, diagnosed, and illustrated. All three species were collected in aquatic to semiaquatic habitats.

The pupal features common to these three species, and to described pupae from New Zealand and South African congeners, are listed and their distribution is discussed within the Tipulidae. Pupal characters indicate a basal position for these subgenera within the Tipulinae; however, none clearly supports the monophyly of *Leptotarsus* as currently classified.

## INTRODUCTION

The crane fly genus *Leptotarsus* comprises over 300 species placed in about 20 subgenera. The group is found in all major faunal regions, including Palaearctic (Oosterbroek and Theowald, 1992:one subgenus, three species); Nearctic (Alexander, 1965:one subgenus, four species); Oriental (Alexander and Alexander, 1973:two subgenera, 11 species); southern Africa and Madagascar (Hutson, 1980:three subgenera, 47 species); South America (Alexander and Alexander, 1970:11 subgenera, 90 species); Australia, New Zealand, and New Caledonia (Oosterbroek, 1989:nine subgenera, 159 species), with greatest diversity in species and subgenera following a Gondwanaland distribution. As noted by Young and Gelhaus (1992), the genus is "doubtfully monophyletic," but nevertheless of great interest due to its probable early origins within the phylogeny of the Tipulinae (sensu Byers, 1992).

As noted for most groups of crane flies in the Southern Hemisphere (Gelhaus and Young, 1991), the immature stages of *Leptotarsus* are poorly known. Descriptions are available for immature of a dozen species in South Africa (Wood, 1952), two species of *Longurio* in North America (Johnson, 1906; Alexander, 1920), and for a few species in the subgenera *Chlorotipula* and *Macromastix* from New Zealand (Rogers, 1927). Habitat varies considerably, ranging from dry soil under various monocotyledonous plants (numerous *Longurio*), forest leaf litter (*Chlorotipula viridis*, see Miller 1971:149), several *Longurio*, several *Macromastix*, rotting wood, including buildings (*Chlorotipula*), and spring runs (North American *Longurio*).

In ongoing studies of Neotropical crane flies, we collected and reared from

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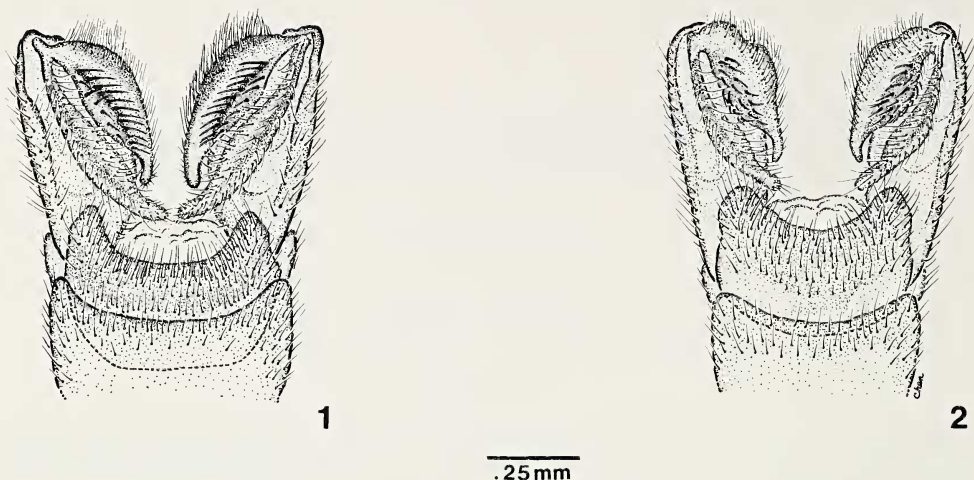


Fig. 1-2.—Male hypopygium of *Leptotarsus (Limoniodes) sulphurellus*. 1, specimen from Ecuador, Province Morona-Santiago, Rio Culebrillas. 2, paratopotype from Ecuador, Abitagua.

aquatic and semiaquatic habitats the previously unknown pupae for two additional subgenera of *Leptotarsus* from South America, *Limoniodes* and *Pehlkea*. In this paper we describe the pupae for a single species in each of these two subgenera, redescribe the pupa of *L. testaceus*, and characterize the pupal instar for the genus.

#### DESCRIPTIONS

##### *Leptotarsus (Limoniodes) sulphurellus* Alexander (Fig. 1-7)

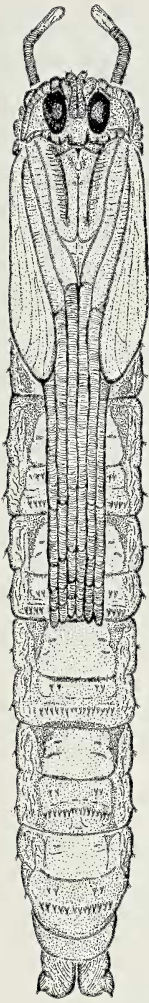
A single species, *L. sulphurellus* Alexander, is known for the subgenus. The reared adults from Rio Culebrillas, Ecuador, are extremely similar to the type specimens from Abitagua, Ecuador, differing in coloration of the darker legs and lack of darkening of the wing tip and stigma. We also note differences in the overall shape of the male inner dististyle and the arrangement of black spines on it between the reared males (Fig. 1) and the paratopotype (Fig. 2). Based on the few specimens available, we don't consider these differences to be of specific value.

**Diagnosis.**—The pupa of *L. sulphurellus* is difficult to recognize as a tipuline except for the wrinkled aspect of the thoracic cuticle (Fig. 4), spines along posterior margins of abdominal pleura, sterna, and terga (spines in rows on terga and sterna, Fig. 3-5), and small spine near base of each male genitalic sheath (Fig. 6). It can be distinguished from nearly all other tipulines by the straight sheath of the maxillary palp (Fig. 3), apices of antennal and maxillary palpal sheaths closely approximated (Fig. 3), and ridges and papillae between the bases of the antennal sheaths (Fig. 3-4).

**Pupal Description.**—Description based on two pupae, one male, one female; two exuviae, one male, one part. Body length ( $N = 3$ ): 16 mm (pupae), 18 mm (exuvia); width 2.1-2.4 mm. Body coloration overall light brown, even in exuviae, slightly darker on head and thorax.

**Head:** Antennal sheath expanded at base, apex of sheath just reaching sheath of prothoracic tibia, narrowly separated from apex of maxillary palpal sheath by half width of leg sheath (Fig. 5). A pair of short, wrinkled ridges lying between base of antennal sheaths, with three pairs of dorsal papillae; first pair most prominent with a single, pale short setae at apex, second more laterad and short, third pair more dorsad and scarcely evident (Fig. 4). Maxillary palpal sheath short, slightly curved at base, then

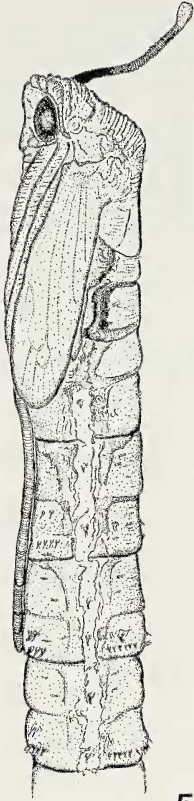
Fig. 3-7.—Pupa of *Leptotarsus (Limoniodes) sulphurellus*. 3-5, habitus: 3, ventral aspect; 4, dorsal aspect; 5, lateral aspect. 6-7, terminal abdominal segments, lateral aspect: 6, male; 7, female.



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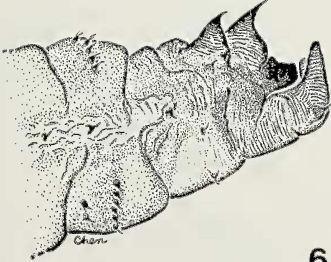


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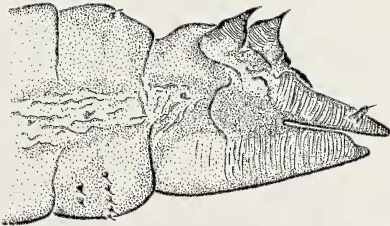


5

1 mm



6



7

1 mm



straight to apex (apex not recurved as in many Tipulinae), base tuberculate (Fig. 5). Distal margin of clypeal sheath slightly emarginate.

Thorax: Respiratory horn length 2.0 mm; base of horn slightly swollen, free length strongly annulate, oriented as in Fig. 4, base of free horn broad and darkened, remainder of stem reddish brown, apex flat and rounded. Dorsum of thorax densely wrinkled, with a pair of ridges transversely oriented in front of respiratory horn attachment, three pairs of short, pale setae on thoracic dorsum opposite base of wing sheath (Fig. 5), several pale setae in small, pale circle directly next to base of wing sheath. Wing sheaths reaching almost to end of abdominal Segment II, venation faint. Leg sheaths side by side, not superposed; apices of leg sheaths reaching middle of Sternum IV in females, and reaching posterior end of Sternum IV in males, prothoracic pair (inner) equal to or only slightly shorter than others (Fig. 3).

Abdomen: Segments II–VII with well-divided basal and caudal annuli. Small spines or spine-tipped tubercles present laterally and near posterior margins of caudal annulus of all segments, placement as in Fig. 3–5. Pleuron III–VII each with anterior and posterior tubercles topped with several very small spines; each posterior tubercle also with a short seta, another seta near tubercle base. Caudal annuli of Segments III–VII with anterior and posterior groups of spines; Sterna III–VII with a pair of close-set anterior spines on each side, each pair with single seta between spines, Sterna III and IV with two widely separated groups of four spines posteriorly, Sterna V–VII with posterior row of 13–17 spines, three pair of setae laterad to each end. Terga III–VII with single anterior spine with seta near base on each side of spine; Terga IV–VII posteriorly with row of 8–14 spines, fewest on VII; four setae anterolaterad of each end of spine row.

Terminal segments: Dorsum of Tergum VIII bare; Tergum IX with spiracles withdrawn into cleft (spiracular yoke, sensu Byers 1961), surrounded by two pairs of spine-tipped protuberances, a minute spine anterolaterad of each anterior protuberance, cleft with two pairs of small papillae in female along margin. Male with a pair of low bumpy swellings between genital sheath and spiny protuberances. Male genital sheaths with two large, curved sheaths, divided unequally near apex, a single tubercle on each near bend beyond base. Female with distinct cercal and hypovalvular sheaths, a single tubercle laterally near each cercal apex.

*Specimens Examined.*—ECUADOR: Prov. Morona-Santiago, Rio Culebrillas, 34 km SE Gualaceo, elev. 2200 m, 22–23 October 1987, wet forest, J. Rawlins, C. Young, R. Davidson, 11 male and two female adults; one male and one female pupae, one male pupal skin with reared adult (Carnegie Museum of Natural History, Pittsburgh).

*Habitat.*—Pupae and pupal exuviae were collected from a saturated, moss-covered, clay substrate along a vertical roadside bank in wet forest. Pupae were positioned in tunnels nearly perpendicular to the surface of the bank, with about one-fifth of the pupa exposed. The soil was not richly organic.

*Leptotarsus (Pehlkea) regina* Alexander  
(Fig. 8–13)

Of the four species placed in this Neotropical subgenus (Alexander and Alexander, 1970), *L. regina* alone exhibits numerous complete to partial crossveins in cells R and M (Alexander, 1914), in addition to the extra crossvein in cell M which is used to distinguish the subgenus (Alexander, 1937). Among the three adults examined here (the two reared females from Ecuador, and the holotype female of *L. regina* from Colombia), there is some variation in the number, placement, and development of these crossveins, as well as the amount of darker patterning along the distal and posterior cells. In addition, there are coloration differences on the head and thorax, possibly related to how teneral the specimens were when preserved. The two pupal specimens also show minor differences. Based on the few specimens available, and the lack of information from male genitalia, we do not treat these as specific differences.

Both reared adults, even when preserved, have greenish tints to the body. This was also noted by Alexander (1914:215) for the holotype female from Colombia.

*Diagnosis.*—The pupa of *L. regina* can be distinguished from those of other known crane flies by the following features: large size, respiratory horn short with



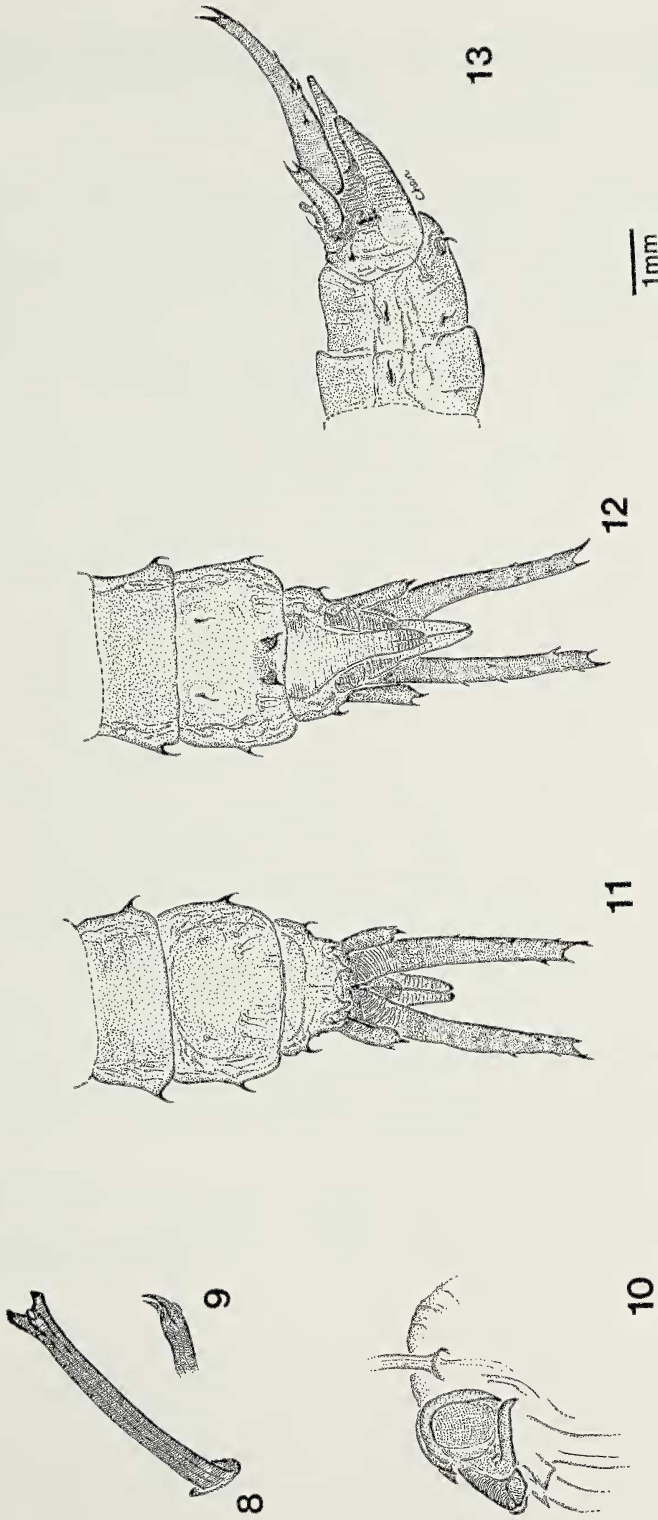


Fig. 8-13.—Pupa (#481) of *Leptotarsus* (*Pehlkea*) *regina*. 8, respiratory horn, dorsal aspect; 9, apex of respiratory horn showing pair of hooks, ventrolateral aspect; 10, head, ventrolateral aspect. 11-13, female terminal abdominal segments: 11, dorsal aspect; 12, ventral aspect; 13, lateral aspect.

apex of each flanked by pair of recurved hooks; few large posteriorly curved spines on abdomen; Sterna VI and VII each with pair of anteriorly directed spines set on large swelling; huge, elongate lobes with forked apices arise at apex of abdomen, each with smaller spines along length.

*Pupal Description.*—Description based on two female pupal skins (#481 and #489). Body length: 33.5 mm (#489)—44.0 mm (#481), width 5–6 mm. Body coloration bright green in life, pupal skins brown, genital sheaths deep reddish brown.

Head: Antennal sheath only slightly expanded at base, narrowed beyond base and tapered to apex; apex lying next to sheath of maxillary palp (Fig. 10). A pair of strong, downward-projecting spines between bases of antennal sheaths, continuous dorsally as a pair of smooth low ridges; a minute dark seta near midlength of each ridge; pale papilla between each ridge and adjacent sheath. Sheath of maxillary palp with slight curve near base, straight medially, then with slight (#481) to strong (near 90°; #489) bend subapically (Fig. 10), base with single tubercle. Distal margin of clypeal sheath narrowly truncate, surface finely striate, with tubercle at base of sheath of each labial palp.

Thorax: Length of respiratory horn 2.4–2.6 mm, base slightly swollen with one long seta, stem of horn of uniform thickness, reddish brown, with indistinct annulations, apex a median slit flanked by a pair of hooks (Fig. 8–9). Dorsum of thorax with only fine transverse lines, deepest around and anterior to mesothoracic respiratory horn; three pairs of short, pale setae on dorsum of thorax medially opposite base of wing sheath, several pale setae in sunken pale circle directly next to base of wing sheath. Leg sheaths side by side, not superimposed; apices of leg sheaths reaching to or near posterior end of Sternum IV, prothoracic pair (inner) only slightly shorter than others. Wing sheaths reaching posterior end of Sternum II, most of venation clearly indicated except numerous supernumerary crossveins; sheath strongly darkened around margin.

Abdomen: Terga and Sterna II–VII with central “clear area” in specimen 489, encompassing area between ventral spines, most pronounced on Sterna III–VII; in specimen 481, pale areas only surrounding base of spines and not including area between spines. Abdominal segments divided into basal and caudal annuli. A few large curved spines (or spine-tipped tubercles) present on pleura and near posterior margins of all segments (Fig. 12–13). Anterior and posterior annuli of Pleura II–VII each with single narrow posteriorly-curved spine, single spine only on VIII, each spine with a minute, pale subapical seta, another long ventral seta near base of posterior spine. Posterior annulus of Sterna III–VII with four large spines, two anterior and two posterior; each anterior spine directed posteriorly, with a single seta; each posterior spine on Sterna III–V large, directed posteriorly, Sterna VI and VII with each posterior spine mounted on a strongly sclerotized, wrinkled swelling (largest in specimen 489), these spines directed anteriorly; surrounding each posterior spine with three anterolateral setae, two of these elongate and pale, median seta minute. Terga I–VI with small spines in two broadly separated groups along posterior margin, each group with 1–4 spines, spines lacking entirely on Terga II and VII (Fig. 11); four elongate, pale setae in row laterad of spines on Terga III–VI and similarly positioned on Terga II and VII; a minute seta anteromedial to each spine group.

Terminal segments: Dorsum of Tergum VIII bare; Tergum IX with spiracular yoke surrounded by two low, lightly sclerotized anterior tubercles and two small anterolateral spines, each spine with a long seta (Fig. 11). Two pairs of reddish, acutely-tipped lobes projecting backward from spiracular area (Fig. 11–13), posterior pair straight and elongate, nearly twice length of cercal sheaths and longer than Segment VII, lateral pair about one-third length of posterior pair; each lobe with several secondary, smaller spines (Fig. 11–13); several pale setae located subapically on each lobe. Cercal and hypovalvular sheaths typical, without additional spines.

*Specimens Examined.*—ECUADOR: Prov. Pichincha, unnamed stream, ~84 km SW Quito (mileage marker #84, old Santo Domingo–Chiriboga road), 00°17'S, 78°54'W, elev. 1400 m, Sept. 7, 1990, J. Gelhaus, R. Bouchard #489, one pupal skin with reared adult (Academy of Natural Sciences, Philadelphia); unnamed stream about 10 km SE Nanegalito (on Calacali–Nanegalito Rd); 00°03'N, 78°35'W, elev. 2000 m; September 4, 1990, J. Gelhaus #481, one pupal skin with reared adult (Academy of Natural Sciences, Philadelphia).

*Habitat.*—Both pupae were collected in fast-flowing, moderate-sized (2–4 m wide, 0.5 m deep) streams, mostly shaded by forest, with predominantly gravel/cobble substrate. The female pupa from field site 481 was collected under a stump drifted in the middle of the stream; it was green in color and quite active. The female emerged on the same day at 1930 hr, the abdomen bright green and remaining so for several hours. The female adult from field site 489 was found

emerging from the pupa in the stream, at approximately 1400 hr; the pupa was lodged against a leafpack along the stream edge off the main run.

*Leptotarsus (Longurio) testaceus* Loew  
(Fig. 14–16)

**Diagnosis.**—The pupa of *L. testaceus* can be distinguished from those of other crane flies by the following features: large size; each respiratory horn elongate, nearly half body length, apex flat with rounded margin; dorsum of Tergum VIII with two pairs of large spine-like curved lobes, all with smaller spines along length; above male genital sheaths, a pair of dome-like swellings with terminal papillae.

**Pupal Description.**—Description based on two male pupae (Georgia specimen in three pieces), and also based on the description of same specimens by Alexander (1920:992, fig. 491). Body length: 42–45 mm, width 3 mm (Alexander, 1920).

**Head:** Antennal sheath (Fig. 14) only slightly expanded at base, surface wrinkled basally, smoother apically, apex nearly touching sheaths of maxillary palp and prothoracic leg. Two strongly ribbed ridges between bases of antennal sheaths; a pair of small papillae lying between sheaths and ridges more dorsally. Maxillary palpal sheath broad throughout, with tubercle near base; sheath straight beyond slight curve near base. Distal margin of clypeal sheath straight.

**Thorax:** Length of respiratory horn 18–19 mm (Alexander, 1920; broken off in Maryland specimen), base swollen, free stem of horn slender, curved beyond base, apex flat with rounded margin. Two large, rounded protuberances in front of respiratory horn, apex of each with single minute papilla. Dorsum of thorax with only fine transverse wrinkles. Apices of leg sheaths “extending to beyond midlength of fourth abdominal segment” (Alexander, 1920), prothoracic pair (inner) much shorter than others, apices reaching only second tarsomere of meso- and metathoracic leg sheaths. “Wing pad reaching end of second abdominal segment; characteristic ventation of genus showing clearly on sheath” (Alexander, 1920).

**Abdomen:** A few large curved spines or spine-tipped tubercles present laterally; shorter spines near posterior margins of all segments. A large, posteriorly curved spine on each basal and caudal annulus of Pleura II–VII, with caudal spine on swelling Segments V–VII, and additional small spine nearby. Each caudal pleural spine with minute pale seta, another long seta ventrolateral near base. Sterna III and IV with two a widely separated rows of six spine-like tubercles, rows along posterior margin; anteriorly, a pair of sublateral low tubercles, each with a long seta. Anterior annuli of Sterna V–VII with a pair of sublateral, wrinkled swellings, each with two close-set spines, one of these minute with single seta; with irregular posterior row of 18, 17, and 11 spines respectively along posterior margin, two setae on sclerotized low tubercles laterad to each end of spine row. Terga III and IV with row of 20–23 strong spines along posterior margin, Terga V–VII with 14–15 spines in row, two setae on small sclerotized tubercles laterad of each end of spine row.

**Terminal segments:** Tergum IX (Fig. 16) with spiracular yoke surrounded by two anterior papillae and two pairs of small anterolateral spines. Two pairs of reddish, acutely tipped, dorsally curved lobes projecting from spiracular area, posterior pair elongate, nearly twice as long as lateral, more anterior pair; each of these lobes with several smaller spines along their length. Two dome-like protuberances between genital sheaths and dorsal lobes, each protuberance with distinct papillae at apex. Male genital sheaths (Fig. 15) large with dorsal curve, a small lateral spine on each near bend (omitted from Alexander, 1920:fig. 491).

**Specimen Examined.**—USA: Georgia, Tallulah Falls, 17 June 1910, J. C. Bradley, (marked as neanotype # 640A, C. P. Alexander), one male exuvia in fluid (Museum of Zoology, University of Michigan, Ann Arbor); Maryland, Cabin John Bridge, 31 May 1900, one male exuvia, dry (Smithsonian Institution, Washington, D.C.).

**Habitat.**—Although *L. testaceus* is one of the larger species of North American crane flies, it is seldom collected and apparently has never been completely reared from larvae. Larvae thought to be this species appear restricted to spring runs and small streams (Byers, 1984), such as “in wet sand in a bog in Maryland” (Alexander, 1920:991, as *Longurio*). Rogers (1930) reported that adults were collected near a “shaded rill,” with a female observed ovipositing along “sandy, grass-and-sedge-grown margin of a small spring rill.” A related species, *L. rivertonensis* Johnson, was collected as adults and un-reared larvae from a “cold”



spring run in New Jersey (Johnson, 1906, as *L. testaceus*; 1909, as *Aeshnasoma rivertonensis*).

## DISCUSSION

### *Monophyly of Leptotarsus*

The pupae of the three species of *Leptotarsus* described here, as well as those described from South Africa and New Zealand, show a great morphological diversity. Nevertheless, certain features are common to these taxa and are discussed below in terms of the strength of evidence for the monophyly and taxonomic recognition of the genus. Comparisons of these pupal characters were made among the three subgenera of *Leptotarsus* herein and to descriptions of South African *Leptotarsus* (*Longurio*) (Wood, 1952) and the New Zealand subgenera *L. (Chlorotipula)* and (*Macromastix*) (Rogers, 1927); additionally, pupae or pupal descriptions were examined for various Limoniinae (*Pedicia*), also taxa discussed by Alexander (1920), and by Oosterbroek and Theowald (1991), and tipulines such as *Brachypremna* (Gelhaus and Young, 1991), *Megistocera* (Rogers, 1949), *Dolichochepeza* (Byers, 1961), *Ozodicera*, *Zelandotipula*, and *Holorusia* (the last three observed in this study).

The following characters, although common to the known pupae of *Leptotarsus*, also occur widely outside the genus: maxillary palpal sheath with apex straight or curved; distal section of antennal sheath short, with apices of antennal and palpal sheaths closely approximated; respiratory horn short to very long but with distinct, annulate stem; dorsum of thorax finely or coarsely wrinkled; abdomen with large spines or spiny tubercles on pleura, sterna, and terga; setal arrangements on abdomen, a spine at or near base of each male genitalic sheath.

A straight or curved maxillary palpal sheath, as seen in *Leptotarsus*, and a few other tipulines (*Megistocera*, *Brychypremna*, *Ozodicera*, *Clytocosmus*) is found throughout the limoniine Tipulidae sensu lato and must be considered plesiomorphic within the Tipulinae (Oosterbroek and Theowald, 1991, character 42); a strongly recurved apex as found in most Tipulinae is undoubtedly the derived condition. *Leptotarsus* pupae in general have closely approximated apices of the antennal and palpal sheaths, although in *Chlorotipula* and some South African *Longurio*, the antennal sheaths extends slightly beyond the palpal apices (Rogers, 1927:fig. 9 shows a greatly elongate antennal sheath of *Chlorotipula* in error). Closely approximated apices of antennal and palpal sheath are seen also in *Brachypremna* and *Megistocera*, both genera also considered with *Leptotarsus* as early lineages within the Tipulinae. The general structure of the respiratory horn of *Leptotarsus* is typical for crane flies (Oosterbroek and Theowald, 1991:character 4.4), yet autapomorphies exist within *Leptotarsus*: elongate (*L. testaceus*), apex with recurved hooks (*L. regina*) and horn minute (*L. micropteryx*, *L. minusculus*; Wood, 1952). Large to small spines on the abdomen are widespread in other Tipulinae, except apparently *Megistocera*, as well as (possibly convergent conditions) in Eriopterini and Hexatomini (Oosterbroek and Theowald, 1991:characters 14 and 53). The anteriorly-directed spines on Sterna VI–VII in *L. regina* must be considered a further autapomorphic derivation. A spine at the base of the male genitalic sheath is found in some Cylindrotomini (*Diogma*, *Triogma*) (Peus, 1952), and a number Tipulinae examined (*Ozodicera*, *Zelandotipula*, *Holorusia*), but is lacking in *Brachypremna* (Gelhaus and Young, 1991).

Certain characters may have applicability for establishing the monophyly of *Leptotarsus* but require more extensive testing against a broad range of tipuline

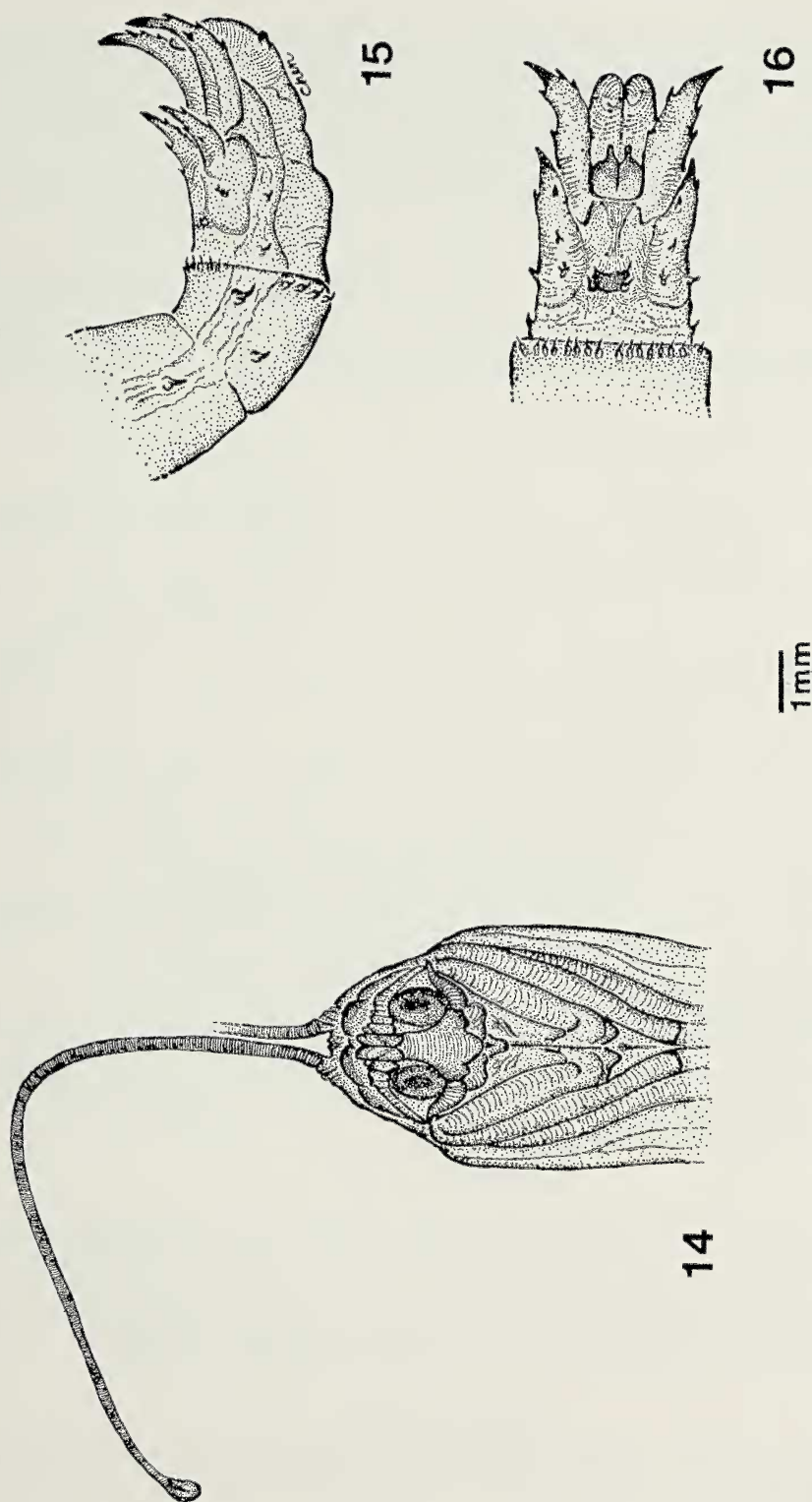


Fig. 14-16.—Pupa of *Leptotarsus (Longurio) testaceus*. 14, pupa, anterior ventral aspect showing respiratory horn. 15-16, male terminal abdominal segments: 15, lateral aspect; 16, dorsal aspect.

pupae. These are: the development of the area between bases of antennal sheaths into ridges, crest, or lobes; several pale setae in pale or sunken area directly dorsolateral to base of wing sheath (this could not be verified in *L. testaceus* due to the poor condition of the specimen, nor it is mentioned in the previous descriptions of any species); and a pair of lobes or swellings dorsad of the male genitalic sheaths. Cephalic papillae are seen also in *Ozodicera*, and the pair of lobes near the male genitalic sheaths are well developed also in *Brachypremna* (Gelhaus and Young, 1991) and *Ozodicera*.

In summary, a few pupal characters (spines and setal arrangement on abdominal terga, sterna, and pleura, spine on male genitalic sheath) show *Leptotarsus* clearly as a tipuline, and other characters, particularly the lack of a recurved apex of the maxillary palpal sheath, indicate that the phylogenetic placement of the genus is basal within the subfamily. We cannot demonstrate the monophyly of the genus at this time based on pupal characters.

#### *Intragenetic Relationships of Leptotarsus*

Although the monophyly of *Leptotarsus* is clearly not supported based on pupal characters, certain features of known pupae indicate possibly close relationships among some subgenera. Within the subgenus *Longurio*, pupae and larvae are strikingly different in morphology and habitat between the South African and North American species. These differences in the pupal instar include, in *L. testaceus*, the elongate respiratory horn (short to minute in South African species), lack of lateral and terminal abdominal spiracles (present in some South African species), large lobes on terminal segment with smaller spines along length (short without additional spines in South African species), and aquatic habitat (fully terrestrial in South African species). The development of a pair of erect forward cephalic lobes indicates the South African species probably have a much closer relationship with subgenus *Chlorotipula* and clearly do not appear to belong in the subgenus *Longurio* based on the type species, *L. testaceus*.

One character, shared possession of spiny terminal abdominal lobes, found in the pupae of *L. (Pehlkea) regina* and *L. (Longurio) testaceus*, indicates that these species have a closer relationship than either has to *Limoniodes* or other *Leptotarsus* (for which pupae are known). In addition, both *Pehlkea* and North American *Longuria* have aquatic immature stages. The spiny terminal lobes, however, are seen apparently also in some *Cylindrotominae* (Peus, 1952). Both *L. regina* and *L. testaceus* have several autapomorphies which may prove to have subgeneric validity, for example, the structure of the respiratory horn, cephalic ridges and abdominal armature, as noted above.

#### ACKNOWLEDGMENTS

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